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Diversity and composition of cactus species along an altitudinal gradient in the Sierras del Norte Mountains (Córdoba, Argentina)

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ABSTRACT

Cacti are important elements of the flora in many ecosystems of the Americas. However, the factors that determine their richness and composition are not well known, particularly at the regional scale. The aim of this work was to study the patterns of cactus richness (both species and growth forms) and composition in the Sierras del Norte mountain range (Córdoba Province, Argentina). Species presence was recorded at 55 sites covering an altitudinal gradient from 203 to 970 m. Twenty four species from eight genera were recorded in the area. Total species richness and growth form richness decreased with increasing altitude. The richness of columnar and short columnar species decreased with increasing altitude, whereas richness of globose species increased. Opuntioid richness did not respond to altitude. Species composition was strongly related to altitude. *Gymnocalycium bruchii* and *Parodia erinacea* occurred at sites located at higher altitudes, whereas at sites at lower altitudes, *Gymnocalycium schickendantzii*, *Stetsonia coryne* and *Cleistocactus baumannii*, among other species, were present. Our results highlight the importance of altitude in shaping the distribution of species and growth forms in the Sierras del Norte Mountains.

1. Introduction

In mountain environments, altitudinal gradients are the main factor influencing vegetation patterns (Körner, 2007). As altitude increases, temperature decreases and irradiance increases, but the effect of altitude on precipitation varies among mountain ranges (Körner, 2007). Some studies report a decrease of species with increasing altitude (Huston, 1994; Rahbeck, 1995; Nogué et al., 2012), whereas other works indicate that the highest richness is found at intermediate altitudes (Grytnes, 2003; Becker et al., 2007). Regarding growth forms, there is a general decreasing pattern of trees and increasing patterns of shrubs and herbs as altitude increases (Pavón et al., 2000). Few studies investigated cactus species richness patterns along altitudinal gradients. Mourelle and Ezcurra (1996, 1997) studied richness and β diversity patterns of cacti but at a very broad geographical scale (e.g. all throughout Argentina). They found that columnar species richness was higher with increasing temperature. Other growth forms, such as globose and opuntioid species, did not respond to variables that could be associated with altitude (e.g., mean annual temperature). Guerrero et al. (2011) found a decrease of endemic cactus richness in a sharp altitudinal gradient in Chile (from 0 to 4000 m). Pavón et al. (2000) analyzed the abundance of growth forms along an altitudinal gradient in central México and found that the abundance of columnar and globose cacti decreases with increasing altitude. None of these studies analyzed changes in species composition along altitudinal gradients.

The mountains of north western Argentina and Bolivia are one of the three main areas of highest cactus diversity in the Americas, together with Mexico and north eastern Brazil (Gómez-Hinostrosa and Hernández, 2000; Hernández et al., 2001; Ortega-Baes and Godínez-Alvarez, 2006). Córdoba Mountains (Fig. 1) can be considered the southernmost portion of the mountains of north western Argentina and Bolivia; the area bears about 31 species of cacti, being the fifth largest vascular plant family by the number of species (Giorgis et al., 2011). With respect to endemisms, from a total of 28 endemic species of Córdoba Mountains, 10 (35%) are cacti (Giorgis et al., 2011). Sierras del Norte, the northernmost range of Córdoba mountains, bears a high richness of cacti species and growth forms; this characteristic, together with an important altitudinal gradient, makes this mountain area and ideal site to study patterns of species distribution. The aims of this work were: 1) to determine the species inhabiting the Sierras del Norte Mountains; 2) to analyze the effect of altitude on species and growth form richness (number of growth forms and number of species of each growth form); and 3) to analyze the effect of altitude on species composition.

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Nomenclature

Hunt (2006)

2. Materials and methods

2.1. Study area

The study area was the Sierras del Norte Mountains, which is the northernmost range of Córdoba Mountains (Fig. 1). The vegetation corresponds to the Mountain Chaco district of the Chaco biogeographic region (Cabrera, 1976). The vegetation along an increasing altitudinal gradient varies from woodlands to shrublands and grasslands (Luti et al., 1979; Giorgis et al., 2011). Due to human disturbances such as fire and grazing, vegetation has been altered, and original woodlands have been replaced by grasslands and shrublands (Zak and Cabido, 2002). At the local scale, vegetation depends strongly on substrate, particularly soil depth and the presence of rocky outcrops (Funes and Cabido, 1995), which is the main habitat of cactus species (Gurvich et al., 2006).

The main environmental gradient in the area is the altitudinal one, ranging from 200 to 1000 m asl. This gradient affects not only temperature, but also precipitation. Mean annual temperature and precipitation vary from 19.3 to 16.2 °C and from 450 to 700 mm, respectively. Frosts are common during winter, particularly at higher elevations (de Fina, 1992).

2.2. Sampling design and data collection

We sampled 55 sites covering the entire altitudinal gradient of the Sierras del Norte Mountains. The sites were also evenly distributed along the whole Mountain Range. Site selection at the different altitudes was determined visually in the field by the presence of rocky outcrops in the landscape, where cacti inhabit (Gurvich et al., 2006, 2008; Dutra Saravia and Souza, 2012). At each site we followed the method of Hernández et al. (2008), with minor modifications. Instead of installing a transect, we walked across each site for 40–50 min, which represents an area big enough (about 3 ha) to find all cactus species. For each site, we recorded all species present, altitude and location with a GPS. Species were classified according to their growth forms into globose, opuntioid, short columnar and arborescent. Unlike in previous classifications (Mourelle and Ezcurra, 1996), we separated columnar species into short columnars (species that reach up to 2 m in height) and arborescent (7–8 m in height). Among arborescent species we included an opuntioid, *Opuntia quimilo*, which can be 6–7 m tall, and presents tree morphology (main stem and developed crown). Species nomenclature follows Hunt (2006).

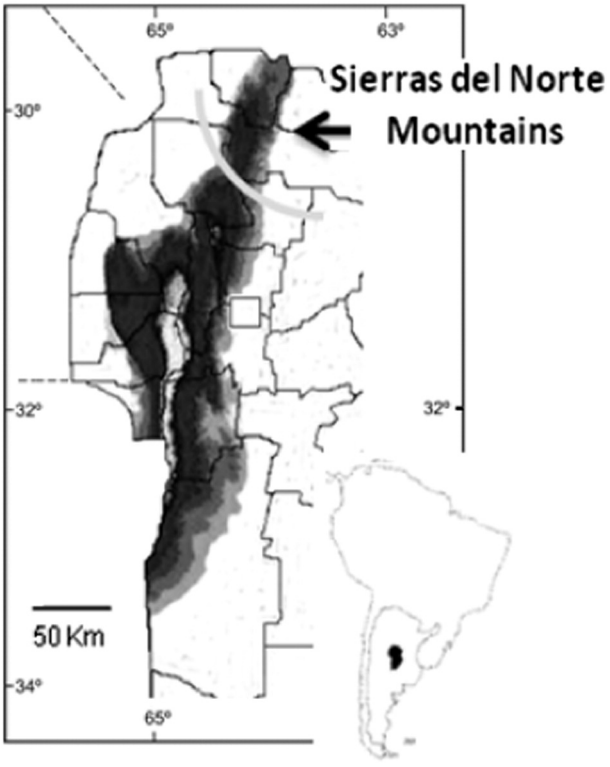

Fig. 1. Location of the Sierras del Norte Mountains in Córdoba province (Argentina). Sample sites were evenly distributed across the region.

2.3. Data analyses

To analyze the effect of altitude on species richness, growth form richness (number of growth forms present at each site) and richness within growth forms (number of species of each growth form at each site), we performed generalized linear models (GLMs). In all cases GLMs were fitted with a Poisson error structure and log link.

The effect of altitude on species composition was assessed in two different ways. Firstly, we performed a Non-metric Multidimensional Scaling (NMDS), using species presence/absence per site matrix and the Jaccard dissimilarity index. NMDS ordination was done using the statistical software package "vegan" version 2.0–6 (Oksanen et al., 2013). NMDS axis were correlated to altitude. The significance of the correlation was assessed using permutation tests ($n = 999$). This was done to analyze the general patterns of species composition in the 55 sites and the relationship between altitude and species composition. Secondly, we calculated β Diversity index (β; Wilson and Shmida, 1984) to analyze the species replacement along the altitudinal gradient with the particular aim to explore whether or not species replacement was gradual along the gradient. To simplify presentation and interpretation of results, instead of comparing all combinations of the 55 sites we summarized them into eight altitudinal belts, and then calculated the index among all pair combinations. We established eight 100 m elevation belts (from 200 to 1000 m). With this simplified matrix we calculated the β diversity index proposed by Wilson and Shmida (1984) between all pairs of altitudinal belts. Wilson and Shmida (1984) β diversity index is calculated with the formula $= (b + c) / 2a$, where $a =$ means number of species across all altitudinal belts; $b =$ number of species that occur in the neighboring belt but not in the focal one; and $c =$ number of species that occur in the focal belt but not in the neighboring one. This index was developed for presence–absence data; it is based on species gains and losses across gradients (Wilson and Shmida, 1984) and can vary between 1 and 0, with values close to 0 meaning that both sites have similar species composition. We then correlated β Diversity index with the "distance" among each combination of belts. For neighboring belts we assigned a value of 1, for belts separated by another belt, a value of 2 and so on.

We also measured Whitakker's β Diversity index (Whittaker, 1960), which is calculated as, ϒ (Gamma)/α (Alfa), with ϒ being the total number of species per altitudinal belt and α the mean number of species per site. This index provides an intra-belt measure of β Diversity.

All statistical analyses were performed with R 2.15.1 (R Development Core Team, 2012).

3. Results

A total of 24 cactus species belonging to eight genera were found at the 55 sites (Table 1), which were located from 203 to 970 m. Eleven species were globose, five were short columnar, three were arborescent

Table 1
List of species, subfamily, growth form, relative frequency and altitudinal range, recorded in Sierras del Norte Mountains, Córdoba province (Argentina).

Species	Growth form	Relative Frequency (%)	Altitudinal range (m a.s.l.) Min–Max	
Subfamily Cactoideae				
Cereus aethiops Haworth	Short columnar	3.6	207	926
Cereus hankeanus K. Schumann	Arborescent	14.5	203	652
Cleistocactus baumannii (Lemaire) Lemaire	Short columnar	14.5	203	565
Echinopsis aurea Britton & Rose	Globose	38.2	203	926
Echinopsis candicans (Salm-Dyck) Hunt	Short columnar	40	296	968
Echinopsis leucantha (Salm-Dyck) Walpers	Short columnar	5.4	207	754
Echinopsis spiniflora (K. Schumann) Berger	Globose	21.8	203	968
Gymnocalycium bruchii (Spegazzini) Hosseus*	Globose	7.3	886	935
Gymnocalycium erinaceum Lambert*	Globose	56.4	203	970
Gymnocalycium monvillei (Lemaire) Britton & Rose*	Globose	12.7	849	970
Gymnocalycium mostii (Gürke) Britton & Rose*	Globose	32.7	346	941
Gymnocalycium quehlianum (F. Haage ex Quehl) Vaupel ex Hosseus*	Globose	12.7	430	797
Gymnocalycium robustum R. Kiesling, O. Ferrari & Metzing*	Globose	3.6	430	437
Gymnocalycium schickendantzii (F. A. C. Weber) Britton & Rose*	Globose	10.9	346	639
Harrisia pomanensis (F.A.C.Weber) Britton & Rose	Short columnar	27.3	203	652
Parodia erinacea (Haworth) Taylor	Globose	18.2	837	951
Parodia mammulosa (lemaire) Taylor	Globose	25.4	754	968
Stetsonia coryne (Salm-Dyck) Britton & Rose	Arborescent	29.1	203	652
Subfamily Opuntioideae				
Opuntia anacantha Spegazzini	Opuntioid	10.9	203	652
Opuntia elata Salm-Dyck	Opuntioid	18.2	430	951
Opuntia ficus-indica (L.) P. Miller	Opuntioid	1.8	633	633
Opuntia quimilo K. Schumann	Arborescent	18.2	344	652
Opuntia salmiana Parm.	Opuntioid	3.6	590	652
Opuntia sulphurea Gillies ex Salm-Dyck	Opuntioid	78.2	203	970

* Species endemic to Córdoba Mountains.

and five were opuntioid. The most frequently found species were *Opuntia sulphurea* and *Gymnocalycium erinaceum* (81% and 56% of the sites, respectively; Table 1). On the other hand, the least abundant species was *O. ficus-indica*, a non-native species that was found in only one site. Other species with low presence were *Gymnocalycium robustum*, *Opuntia salmiana* and *Cereus aethiops*, which were found only at two sites (4%). Six of the species, all from the genus *Gymnocalycium* (*G. bruchii*, *G. monvillei*, *G. erinaceum*, *G. mostii*, *G. robustum* and *G. quehlianum*), are endemic to Córdoba Mountains, and two of them (*G. robustum* and *G. erinaceum*) are endemic to this range.

The altitudinal range varied among species, even within growth forms (Table 1). With the exception of arborescent species, all the growth forms presented at least one species along the entire gradient. Arborescent species were absent at an altitude of about 600 m. Among globose species, different patterns were found. Some species, such as *G. erinaceum*, had a wide altitudinal range, whereas *G. bruchii*, *Parodia erinaceae* and *G. monvillei* presented narrow ranges. Arborescent forms were present only at low altitudes, whereas opuntioids and short columnar species did not present clear patterns.

Species richness varied from 1 to 11 species per site, with a mean of 5 species. Total species richness, arborescent species richness, and short columnar species richness were negatively related to altitude (Table 2, Fig. 2), whereas globose species richness were positively related to altitude. Opuntioid species richness was not significantly related to altitude.

Cacti species distribution along the NMDS axes responded to an altitudinal gradient (Fig. 3), since altitude was negatively related to axis 1 according to the permutation test ($r^2 = 0.72$; $p \leq 0.01$). The most characteristic species of the higher sites were *G. monvillei*, *G. bruchii* and *Parodia erinacea*: all of them globose species. On the other hand, the sites at lower altitudes were characterized by species such as *Stetsonia coryne*, *Cleistocactus baumannii* and *G. schickendantzii*, which belong to different growth forms.

β diversity varied from 0 to 0.97 among the altitudinal belts (Table 3). In general, β diversity was low between contiguous altitudinal belts, as expected, but particularly at 700 m, β increased notoriously, indicating a sharp change in species composition. Accordingly, β diversity was positively correlated ($r^2 = 0.7$; $p \leq 0.001$) to the distance among altitudinal belts (Fig. 4). However, values corresponding to the sites at 700 m were much higher (Fig. 5).

Fig. 5 shows α, ϒ and Whitakker β Diversity index. Beta diversity is relatively higher in the lower altitudinal belts, high at intermediate (500–599 and 600–699) belts, and intermediate at the two higher altitudinal belts. ϒ diversity is also higher at intermediate altitudinal belts.

4. Discussion

The cactus flora of the Sierras del Norte Mountains comprises 24 species, which represent 77% of all cacti present in the Córdoba

Table 2
Generalized Lineal Models (GLMs) performed between Altitude and all Richness variables.

	β	SE	Z	P	r^2
Species richness	−0.0005	0.0002	−1.928	0.0539	0.67
Arborescent species richness	−0.0047	0.0008	−5.695	1.24e−08	0.44
Short columnar species richness	−0.0019	0.0006	−3.096	0.00196	0.19
Globose species richness	0.0011	0.0004	2.654	0.00795	0.56
Growth form richness	−0.0007	0.0003	−2.021	0.04	0.75
Opuntioid species richness	−0.0003	0.0005	−0.51	0.6	0.01

β, coefficient estimate; SE, standard error; Z, z-statistic; P, probability; r^2, R-squared.

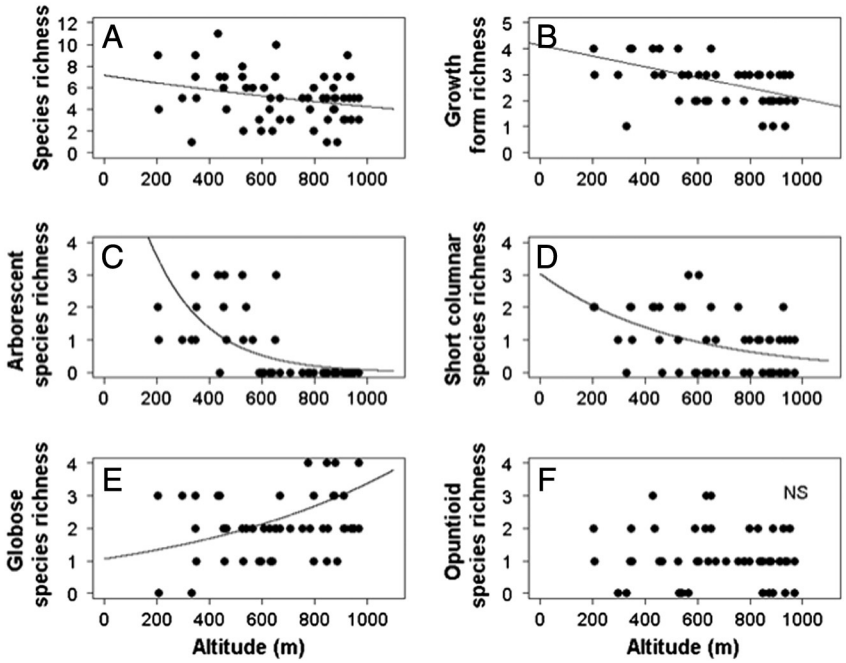

Fig. 2. Relationship between Altitude (m) and Species richness (A), Growth form richness (B), Arborescent species richness (C), Short columnar species richness (D), Globose species richness (E) and Opuntioid species richness. The black line is the statistically best fitted GLM model of the relationships. Each dot represents a site (n = 55).

Mountains and about 10% of all species present in Argentina. Moreover, from the 10 cactus species endemic to Córdoba Mountains, six are present in this range, and two are even endemic to it (*G. robustum* and *G. erinaceum*; Pilbeam, 1995). We found that species richness decreased with altitude. Many studies highlighted the effect of altitude on plant species richness (Becker et al., 2007) and found basically two main patterns: a decrease of richness with increasing altitude, and a humpback relationship, with richness reaching a peak at intermediate altitudes (Grytnes, 2003; Becker et al., 2007). Particularly in cacti, the only study that analyzed species richness along and altitudinal gradient is that of Guerrero et al. (2011), who found a decrease of endemic species richness as altitude increases. Although those authors did not explain this pattern, it is likely that the extreme aridity in that area, together with the fact that coastal areas receive humidity from the ocean, in the form of fog, would explain the higher richness of species at low altitudes and a sharp decrease as altitude increases.

The decrease in growth form richness with altitude is consistent with results reported by Pavón et al. (2000). In our study this pattern is explained by the decrease of arborescent and short columnar species with increasing altitude. These results support the assumption that growth forms respond differentially to climate, particularly to low temperatures (Yeaton and Cody, 1979; Nobel, 1980a; Nobel, 1982; Mourelle and Ezcurra, 1996; Flores and Yeaton, 2003). The explanation to this pattern is that shorter growth forms uncouple their temperature from that of the air (Körner, 1999). Due to this phenomenon, low temperatures affect columnar species to a greater extent, reducing their growth and survival (Nobel, 1980b), which in turn limits their distribution into colder areas. In the case of species that grow close to the soil surface, such as globose and some opuntioid species, body temperature can be much higher than the temperature of the surrounding air, avoiding the effect of low temperatures, and therefore allowing plants to grow and persist in colder areas (Körner, 1999). However, more physiological studies are needed to confirm that this mechanism explains this pattern. Unlike previous works that reported a decrease of globose species with altitude (Pavón et al., 2000), we found an increase. Few studies analyzed distribution patterns of globose species. Mourelle and Ezcurra (1996) found that globose species richness was positively associated with mountain environments. Other studies found that even in mountain areas, those species are particularly associated with rocky outcrops (Gurvich et al., 2006; Dutra Saravia and Souza, 2012). The fact that we found an increase of globose species with altitude suggests that some

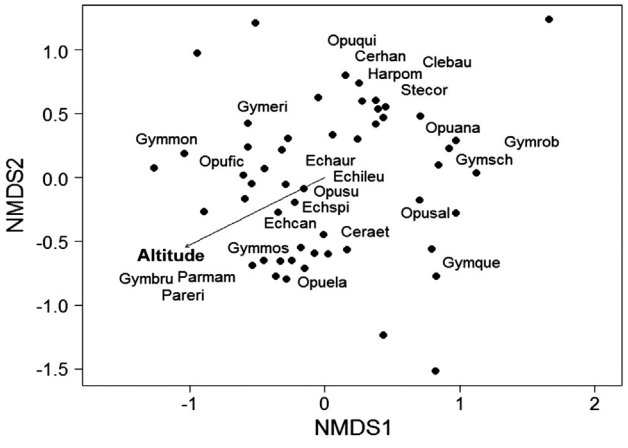

Fig. 3. Triplot and fitted surface of Altitude from a Non-metric Multidimensional Scaling (NMDS) of the 55 sites × 23 cacti species of Sierras del Norte Mountain, Córdoba. Stress values were 0.17 of this data set. Species abbreviations correspond to the first three letters of the genus and species detailed in Table 1. Each circle represents one site (n = 55).

Table 3
Beta Diversity index among all combinations of the eight altitudinal belts. For this analysis we summarized the 55 sites in eight altitudinal belts. Light shaded area indicates low species turnover (β < 0.33); dark shaded area indicates high species turnover (β > 0.66; sensu Mourelle and Ezcurra, 1997).

	300–399	400–499	500–599	600–699	700–799	800–899	900–1000
200–299	0.28	0.49	0.49	0.56	0.70	0.90	0.83
300–399		0.21	0.14	0.28	0.70	0.90	0.90
400–499			0.14	0.28	0.63	0.97	0.97
500–599				0.14	0.63	0.97	0.97
600–699					0.63	0.97	0.97
700–799						0.35	0.35
800–899							0.00

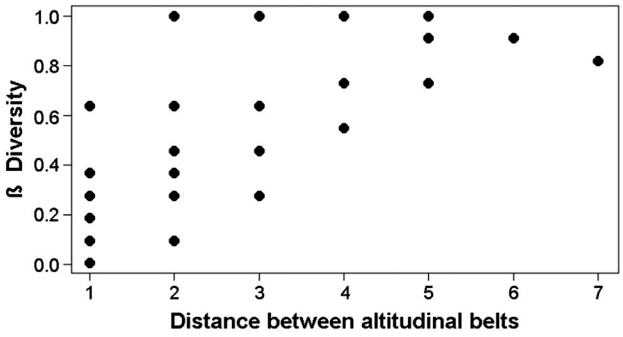

Fig. 4. Relationship between distance among altitudinal belts and Beta diversity (Wilson and Shmida, 1984). A distance value of 1 corresponds to neighboring altitudinal belts, distance values of 2 correspond to altitudinal belts separated by one another, and so on.

globose species are not tolerant to drier and/or warmer environments. Probably, the reason why they can support low temperatures is not an advantage in warmer environments. Martorell and Patiño (2006) found that globose cactus species inhabiting at lower altitudes are present in cliff environments, where temperature is cooler than in surrounding flat areas. This result supports the hypothesis that globose species distribution would be constrained by high temperatures, but further studies are needed to confirm this pattern. We also found that richness of opuntioid species did not respond to altitude. To our knowledge, no study analyzed the distribution of this group in relation to altitude (Illoldi-Rangel et al., 2012). This group is particularly diverse in South America, occupying a wide variety of environments, from sea level to more than 4000 m, and from humid to very dry environments (Anderson, 2001). Opuntioid species are one of the cacti, or even plant species, that can tolerate the widest range of temperatures. *Opuntia fragilis*, a species that inhabits the prairies of the USA and Canada, was found to tolerate temperature ranges from 55 to −196 °C under laboratory conditions (Ishikawa and Gusta, 1996).

Very few studies analyzed variations of cactus communities in relation to environmental variables. Dutra Saravia and Souza (2012) analyzed species composition of cacti from Southern Brazil in relation to some environmental variables (e.g., rock and soil) and land use. In our study we found that species composition was strongly related to altitude. We can broadly separate two main communities: those at low and at high elevations, from 200 to 700, and from 700 to 1000 m, respectively. This limit coincides with the upper limit of arborescent species. The communities at high elevation are characterized mainly by globose species, such as *G. monvillei*, *G. bruchii* and *P. erinacea*. On the other hand, communities at lower elevation are richer in growth forms, and are characterized by species such as *S. coryne*, *G. robustum* and *Harrisia pomanensis*. The mean annual temperature of this boundary area is of about 17.5 °C (de Fina, 1992). Our study highlights the importance of analyzing the species composition together with other variables, such as richness or diversity, because, as we show, they responded differentially to altitude. These results agree with the β diversity analyses. We found that β diversity is generally low between contiguous altitudinal belts, and high between distant ones. However, there is a particular point along the gradient, at 500 m, where species turnover is particularly high. This indicates that changes in species composition along the gradient are not gradual. These non-linear patterns seem to be very common in the response of vegetation to environmental variables (Hemp, 2006; Danz et al., 2012). Whitakker β Diversity index was higher at intermediate altitudinal belts and remained relatively high at higher belts. This pattern could be attributed to a higher environmental heterogeneity as altitude increases. ϒ Diversity (total number of species per altitudinal belt) was higher at intermediate belts, which is a result of the contact of the cactus species occurring at low and high altitudes.

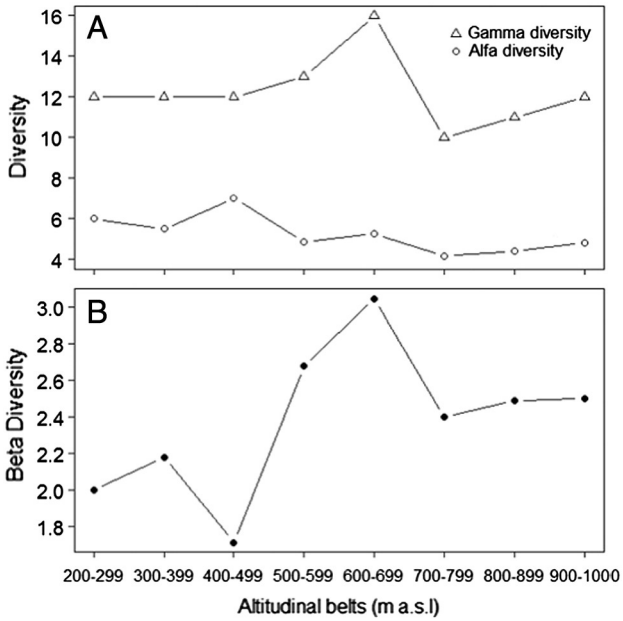

Fig. 5. Alfa, Gamma (A), and Whittaker (1960) Beta (B) indices of each altitudinal belt.

Although it is not possible to separate the effects of temperature from those of precipitation, it is more likely that the main patterns found in our study are related to temperature rather than to precipitation, as we already discussed. However, it is possible that that different species would respond differentially to the combination of these two factors. For example, the absence of species below their altitudinal range could be due the lower precipitation there or the combination of lower precipitation and higher temperatures (higher evapotranspiration). On the other hand, at higher altitudes the absence of species typical of lower altitudes is likely due to the lower resistance of those species to low temperatures. However, cacti are particularly susceptible to rooting, which is more frequent in humid conditions. So, we cannot discard that the absence of species typical of lower elevations in higher ones could be explained by this process. Further studies are needed to understand the possible mechanisms underlying this pattern. Similar studies in mountains with different trends in precipitation could also give clues about the effects of these factors on cactus distribution.

Our results highlight the importance of the Sierras del Norte range in the conservation of the cactus flora of Córdoba Mountains. Many species of this family are under conservation risks (Boyle and Anderson, 2002; Ortega-Baes et al., 2010), and species from Córdoba Mountains do not escape this situation. Although populations of all species found in this work seem healthy, illegal collection is becoming frequent and human activities (mainly grazing and wildfires) are probably affecting populations in the area (Gurvich et al., 2006). However, in the entire range there is only one Natural Reserve of only 3000 ha, Cerro Colorado Provincial Reserve, located at a low altitude (from 500 to 700 m). It is clear that this reserve is not effective in protecting the whole cactus flora, so more private or public reserves would be needed, taking into account the different altitudinal belts. Another problem that cacti face is that imposed by climate change. Climatic models of Central Argentina predict and increase in temperature, but particularly during winter, and also an increase in precipitation (Nuñez, 2006), which can greatly affect species distributions (Téllez-Valdés and Ávila-Aranda, 2003).

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